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SUPPLEMENTARY NOTES ON THE SYSTEMATICS OF CHAETOGNATHA[1]

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With 3 Text-figures

I have already shown an idea of the taxonomical outline of Chaetognatha in the preceding volume of this journal (XII, No. 5, 1965, pp. 335-357); there it is stated that the pelagic forms of a simpler body structure seem to be derived from the littoral forms with creeping ability and with more complicated body structures and that the existence of the ventral transverse musculature is regarded as a basic feature separating the primitive forms from the advanced ones and the tooth apparatus of *Krohnitta* is considered to be a sign showing a high grade of specialization (p. 341), but no further reasons being given for such considerations. On the other hand, I gained a copy of Mrs. ALVARIÑO's very important paper, "Quetognatos epiplanctonicos del Mar de Cortes" (Revista de la Sociedad Maxicana de Historia Natural, XXIV, 1963, pp. 97-203), after my manuscript had been laid under editorship; her opinion of grouping the species of *Sagitta* according to their morphological similarities or ecological affinities (pp. 136-141) is to be appreciated very highly, but the comparison between hers and mine was not made in my last paper. The present paper is prepared to make up for the above-mentioned insufficiency.

I. The primitiveness of the littoral species

a) *Ventral transverse musculature*: This musculature is found in the Phragmophora and assumes a membrane or diaphragma stretched across the body coelom between the dorsal edge of the lateral field or the lateral edge of the dorsal longitudinal muscle bands and the ventro-median line. The exact function of this musculature is not known yet. So far as concerned with the pelagic phragmophorans such as *Eukrohnia* spp., this structure seems quite useless for these animals; very probably this remains as a vestigial structure in them. For the sagittiform animals, the creeping seems to require

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much more complicated and delicate movements of body parts than the swimming does. Moreover, individuals of *Spadella* are known to keep their anterior half of the body raised while they adhere to the substratum by the ventral surface of the posterior half of the body ; this posture is taken when the animals are waiting for preys or a couple of them are in mating. The ventral transverse musculature is considered to be effectual to keep the body rigid for raising the anterior half of the body or to make the complicated or delicate movements necessary for creeping possible in cooperation with the longitudinal muscle bands.

b) *Bathypelagic chaetognaths*: All the six species of Eukrohniidae and *Solidosagitta zetesios* and *marri* and *Caecosagitta macrocephala* are referred to the bathypelagic chaetognaths in a strict sense, although some species of *Mesosagitta* and *Flaccisagitta* and *Solidosagitta planctonis* may often be found in meso—to bathypelagic fauna. Of these bathypelagic chaetognaths, the forms else than the members of Eukrohniidae belong to the Ctenodontina of Aphragmophora. Evidently they are considered to be derived from the epipelagic form of the same group and having settled in the deeper stratum possibly through the medium of the process of some kinds of vertical migrations. As the morphological specialization, though only the diminution or degeneration of some components of the eye is known with certainty, has occurred in bathypelagic ctenodontids, the reversal course of evolution from the bathypelagic form to the epipelagic one is hardly suggestible. On the other hand, members of Eukrohniidae are all provided with the ventral transverse musculature and without exception furnished with some glandular structures on the body surface; these features are common to Eukrohniidae and Spadellidae. It is very difficult to define the function of these glandular structures exactly, but it seems apparent that the ventral transverse musculature is now quite functionless in these pelagic forms. The quite absence of any forms allied to these families in the rich epipelagic chaetognath fauna seems to allege that Eukrohniidae is derived from Spadellidae and has moved from the littoral habitat directly to the bathypelagic life. And the constant environments of the deep waters and the sparse population have retarded the evolution and thus some ancestral morphology is still now retained. Also in this case, the morphological specialization—some trend toward the degeneration of the eye or reduction of glandular structures on the body surface—is confined to Eukrohniidae, thus the process from the bathypelagic life to the littoral is improbable.

II. The natal place of Chaetognatha

a) *Home sea of Chaetognatha*: Nine species are known from the Antarctic and the subantarctic seas, of which three—*Eukrohnia bathyantarctica, Solidosagitta*

Table 1. Distributions of chaetognaths in the world seas.

	Indo-Pacific	Antarctic	Atlantic
Amiskwia sagittiformis	+		
1. *Spadella cephaloptera*	+		+
2. *Spadella angulata*	+		
3. *Spadella moretonensis*	+		
4. *Spadella schizoptera*	+		+
5. *Spadella sheardi*	+		
6. *Spadella johnstoni*	+		
7. *Spadella nana*			+
8. *Spadella pulchella*			+
*9. *Eukrohnia hamata*	+	+	+
*10. *Eukrohnia fowleri*	+	+	+
*11. *Eukrohnia bathyantarctica*		+	
*12. *Eukrohnia bathypelagica*	+		
*13. *Heterokrohnia mirabilis*	? +	+	
*14. *Bathyspadella edentata*	+		
15. *Sagitta bipunctata*	+		+
**16. *Sagitta setosa*			+
**17. *Sagitta setosa* var. *euxina*			+
**18. *Sagitta tenuis*	(+)		+
**19. *Sagitta friderici*	(+)		+
20. *Sagitta helenae*			+
**21. *Sagitta bombayensis*	+		
**22. *Zonosagitta bedoti*	+		
**23. *Zonosagitta bedoti* f. *minor*	+		
**24. *Zonosagitta bedoti* f. *littoralis*	+		
25. *Zonosagitta pulchra*	+		
26. *Serratosagitta serratodentata*	+		+
27. *Serratosagitta pesudo-serratodentata*	+		
***28. *Serratosagitta tasmanica*	+	(+)	+
***29. *Serratosagitta bierii*	+		
30. *Serratosagitta pacifica*	+		
**31. *Parasagitta elegans*	+		+
**32. *Parasagitta elegans arctica*			+
**33. *Parasagitta elegans baltica*			+
**34. *Parasagitta hispida*			+
**35. *Parasagitta hispida americana*	(+)		
36. *Parasagitta robusta*	+		
37. *Parasagitta ferox*	+		+

Table 1. (continued)

	Indo-Pacific	Antarctic	Atlantic
38. *Aidanosagitta neglecta*	+		
**39. *Aidanosagitta oceania*	+		
**40. *Aidanosagitta johorensis*	+		
41. *Aidanosagitta regularis*	+		
**42. *Aidanosagitta bedfordii*	+		
**43. *Aidanosagitta demipenna*	+		
**44. *Aidanosagitta crassa*	+		
**45. *Aidanosagitta crassa* f. *naikaiensis*	+		
**46. *Aidanosagitta crassa* f. *tumida*	+		
**47. *Aidanosagitta delicata*	+		
**48. *Aidanosagitta tropica*	+		
49. *Aidanosagitta parva*	+		
50. *Mesosagitta minima*	+		+
51. *Mesosagitta decipiens*	+		+
52. *Mesosagitta neodecipiens*	+		
53. *Solidosagitta planctonis*	+		+
*54. *Solidosagitta zetesios*	+		+
*55. *Solidosagitta marri*		+	
*56. *Caecosagitta macrocephala*	+	+	+
57. *Flaccisagitta hexaptera*	+		+
58. *Flaccisagitta enflata*	+		+
59. *Flaccisagitta gardineri*	+		
60. *Flaccisagitta lyra*	+		+
***61. *Flaccisagitta scrippsae*	+		
62. *Flaccisagitta gazellae*		+	
***63. *Flaccisagitta maxima*	+	+	+
64. *Pterosagitta draco*	+		+
65. *Krohnitta subtilis*	+		+
66. *Krohnitta pacifica*	+		+
Number of species	55	9	31

*···Bathypelagic, **···of the Neritic waters, ***···of the Special water masses.
The parenthesized are forms immigrated from other seas.

For *Zonosagitta bedoti* f. *littoralis* refer TOKIOKA and PATHANSALI (1965): A new form of *Sagitta bedoti* BÉRANECK found in the littoral waters near Pennag (Bulletin of the National Museum Singapore, No. 33, Part 1, 5 pp., 1 text-fig., 2 tables).

marri and *Flaccisagitta gazellae*—are endemic to these areas, while others, *Eukrohnia hamata, Eukrohnia fowleri, Heterokrohnia mirabilis, Serratosagitta tasmanica, Caecosagitta macrocephala* and *Flaccisagitta maxima* are distributed in other seas, too. Of the 62 taxa, of which the validity was admitted in my previous paper, 54 occur in the Indo-Pacific, while 31 in the Atlantic including the Mediterranean Sea and the Black Sea. There are 31 endemic forms in the Indo-Pacific, while only 8 endemic ones in the Atlantic. The single record of *Heterokrohnia mirabilis* from the depths of the trench east of Tisima (the Kurile Islands) is not of the absolute definitiveness. The distributions of *Sagitta tenuis, Sagitta friderici* and *Parasagitta hispida* f. *americana* in the nearshore waters of the east Pacific off the southern California to north South America may be regarded as the extension of the Atlantic chaetognath fauna invaded the Pacific through the passage ever opened in Central America in the earlier time not so far ago. On the other hand, a few Indo-Pacific species which may appear very rarely west or north-west of the Cape of Good Hope being carried there by the Agulhas Current are excluded from the Atlantic chaetognath fauna. Even though these points are taken into the consideration, the predominance of the Indo-Pacific chaetognath fauna can not be doubted. Actually the predominance of the Indo-Pacific species can be seen in many of genera as shown in Table 2.

Table 2. Number of species of respective genera in the Pacific and the Atlantic.

	Indo-Pacific	Atlantic
Spadella	6 (4)	4 (2)
Eukrohnia	3 (1)	2
Heterokrohnia	1	
Bathyspadella	1 (1)	
Sagitta	4 (1)	6 (3)
Zonosagitta	4 (4)	
Serratosagitta	5 (3)	2
Parasagitta	4 (2)	5 (3)
Aidanosagitta	12 (12)	
Mesosagitta	3 (1)	2
Solidosagitta	2	2
Caecosagitta	1	1
Flaccisagitta	6 (2)	4
Pterosagitta	1	1
Krohnitta	2	2
	55 (31)	31 (8)

The parenthesized are of the endemic species.

Only in two genera, *Sagitta* and *Parasagitta*, the Atlantic species are predominant. Contrarily the complete absence of *Zonosagitta* and *Aidanosagitta* in the Atlantic is very impressive. Borrowing the MATTHEW's theory partially to this case, the home sea of the Chaetognatha may be presumed to be in the Indo-Pacific. The fact that the fossils of the only possible ancestral chaetognath, *Amiskwia*, were found in British Columbia of Canada may be taken to support the present supposition.

b) *Natal area of Chaetognatha in the Indo-Pacific*: Of the Pacific 55 forms, 25 are distributed in the open oceanic area and epi to meso-planktonic, although 4 of them *Serratosagitta tasmanica*, *Serratosagitta bierii*, *Flaccisagitta scrippsae* and *Flaccisagitta maxima* are apparently confined respectively to the special water masses, generally the transitional or subpolar mixing water masses and those affected by them. Thus the pure open oceanic forms spread widely throughout the temperate to tropical waters are reduced to 21. On the other hand there are 17 forms inhabiting the inlet or the neritic waters; *Parasagitta elegans* is treated here as a member occurring most frequently and densely in the subarctic to arctic neritic waters. Six species of *Spadella* are known from the Indo-Pacific. As species of Eukrohniidae are phylogenically related closely to Spadellidae, they may be treated here in the group of littoral forms. Then the littoral—neritic forms attain 28 in total. Bathypelagic *Solidosagitta zetesios* and *Caecosagitta macrocephala* are regarded to belong to the open oceanic forms. Thus the extant littoral—neritic taxa are nearly as rich as the oceanic taxa in the Indo-Pacific.

Table 3. Distributions of species in the Indo-Pacific and the Atlantic.

	Indo-Pacific	Atlantic	Total
Littoral	6	4	8
Bathypelagic	7	4	7
Neritic*	17	8	22
of Special water masses	4	2	4
Oceanic, epi-mesopelagic	21	13	22

* Including *Parasagitta elegans*.

In the Atlantic are known 15 oceanic epi-mesoplanktonic forms, including *Serratosagitta tasmanica* and *Flaccisagitta maxima* both limited to the special water masses as in the Indo-Pacific. Bathypelagic *Solidosagitta zetesios* and *Caecosagitta macrocephala* are added to the oceanic group. For the littoral—neritic group, there are 6 phragmophorans and 8 inlet-neritic aphragmophorans. If such a comparison is made solely on the endemic forms, then the ratio littoral-neritic forms: oceanic forms will be 19:11 in the Indo-Pacific and 7:1 in the Atlantic. Then throughout the world seas, there are

14 phragmophorans and 22 inlet—neritic aphragmophorans, while 26 oceanic aphragmophorans, including 2 bathypelagic and 2 antarctic—subantarctic species, and 4 forms limited to the special water-masses are known. Thus 36 forms are enumerated for the littoral—neritic group, while 30 for the oceanic group.

Table 4. Distributions of endemic species in respective oceans.

	Indo-Pacific	Antarctic	Atlantic
Littoral	4		2
Bathypelagic	2	2	
Neritic	14		5
of Special water masses	2		
Oceanic, epi-mesopelagic	9	1	1
	31	3	8

Such relative abundance of the littoral—neritic taxa, this may be accepted as the absolute dominance when the extensions of the littoral—neritic and oceanic areas are compared each other, and especially the occurrences of rich endemic species in the neritic waters seem to show that the neritic part of the sea is the point of original dispersal for chaetognaths, where the specific differentiation has been most progressive (MATTHEW, 1915). In this case, of course, the environmental conditions, so variable topographically and seasonally and rich of biological competitors, of the neritic waters have apparently favoured the specific differentiation in that area, too. Further fundamentally, the shallow littoral waters must ever be the cradle for all living organisms, although the tracing back to so remote antiquity is quite useless at present.

On the other hand, specialization seems to be advanced in the open oceanic area which must be periphery of the dispersion for this animal group. *Aidanosagitta*, strictly limited to the Indo-Pacific and mostly inhabitting the neritic waters, is the most dominant group of the Aphragmophora and characterized by the longer tail segment and the corona ciliata not attaining anteriorly beyond the level of the eyes. These features may be considered as representing some of the characteristic structures of the littoral chaetognaths. This phenomenon reminds us of some cases availed by MAYER (1963) to establish his theory that in the intraspecific spectation, original phenotypes are found in the main body or the central part of the species range, whereas the secondary deviations are seen in the peripheral populations, especially in peripheral isolated populations*. Contrarily, the occurrence of *Flaccisagitta*, whose flaccid appearance is considered to be a sign of the

* HILLENIUS, D. (1964): Periphery and archaic forms. Beaufortia, Vol. 11, No. 138, pp. 75–83, 2 maps.

structures most adapted to the pelagic life, is limited to the far oceanic waters.

Then what is the relation between the planktonic forms in the neritic waters and the littoral benthonic forms? Most of the metazoan plankton groups have respectively non-pelagic companions of the same group or the closely related groups, and these are always much richer than the pelagic ones in number of species, but in the Chaetognatha which is quite an independent group and contains the benthal forms occupying only a small part of the whole species. I don't intend to go back so remote ancestral age as HADŽI* (1964) does to explain his opinion that the pelagic organisms were ever derived from the benthal organisms. Only in the case of this animal group, it is not impossible that the planktonic animals sank to the sea floor and were adapted to be the benthonic forms. However, the differences between the pelagic aphragmophorans and the benthonic phragmophorans are so remarkable; the latter is much more complicated in the structure and more heavily furhished with glandular structures over the body surface than the former of a simple structure fitting the pelagic life. The acquisition of the ventral transverse musculature, many of glandular structures, and of much stouter texture by sinking down to the benthonic life is not impossible, but very improbable throughout the general phenomena prevailing in the nature. Losing of these complicated structures to fit the pelagic life is much more acceptable.

Summing up the above-mentioned inferences, it may be concluded that chaetognaths were originally the creeping benthonic animals inhabitting the shallow littoral areas of the temperate—tropical parts of the former sea covering the today's Indo-Pacific, some of them went down to the depths and became to be bathypelagic phragmophorans which retain still some significant primitive features characteristic to the creeping life, in the permanent stable environments. Some other members rose up to the neritic plankton life; their structure was modified to be adapted to the pelagic life by losing by and by the ventral transverse musculature and some glandular structures on the body surface, diminishing the thickness of the musculature, and by developing the fin system; then they extended towards the offshore oceanic waters differentiating themselves into a certain number of species. The oceanic circumstances, though the water is quite continuous throughout the world seas, comprise some different water masses which respectively afford a special different environment to the immigrated animals. A few of the oceanic aphragmophorans, then went down to the bathypelagic life. In the Indo-Pacific, most of the neritic and planktonic chaetognaths belong to the

* HADŽI, J. (1964): Genetic relationship between pelagic and benthal organisms. Acta Adriatica, Vol. 11, pp. 121–126.

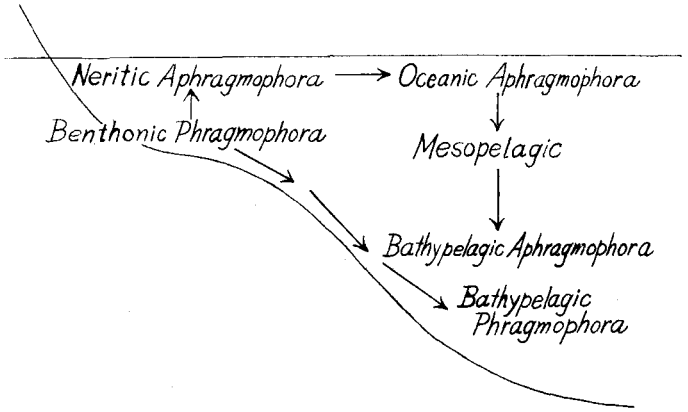


Fig. 1. Diagram showing the processes of evolution from the benthonic Phragmophora to respective pelagic forms. The secondary invasion of the oceanic Aphragmophora to the neritic waters is possible as shown by *Sagitta tenuis*, *S. friderici*, *S. setosa* and *Parasagitta hispida* in the Atlantic.

genus *Aidanosagitta*, whereas in the Atlantic they are represented by members of *Sagitta*, which possibly show the secondary invasion into the neritic waters.

III. Phylogeny within respective orders

Needless to say about the primitiveness of the Spadellidae in the order Phragmophora. Of the Eukrohniidae, *Bathyspadella* is considered to be the nearest to the Spadellidae, as its unusually large tail segment reminds us of that of the littoral creeping forms. Nothing can be mentioned about which of *Eukrohnia* and *Heterokrohnia* is more primitive.

Then the problem lies in the phylogeny within the order Aphragmophora. In the Ctenodontina, the Pterosagittidae seems to be more primitive than the Sagittidae because of its larger tail segment and the corona ciliata confined to the neck region. The existence of only the posterior pair of lateral fins, beginning at the trunk-tail septum, may be taken as one of the primitive features prevailing in Spadellidae. The extensive collarette does not seem to imply any phylogenically significant specialization. Rather it is considered that this structure started in the Spadellidae and developed in some neritic aphragmophorans as seen in *Sagitta bombayensis* LELE and GAE and *Aidanosagitta crassa* (TOKIOKA). Originally this might be useful as a protective tissue, but in the extensively developed state it may be effective to enhance the bouyancy of the animals of a moderate size; generally pelagic animals of much smaller sizes won't need such a structure. *Aidanosagitta regularis* (AIDA) furnished with a strongly developed collarette is evidently an oceanic species drifted out from the neritic populations. The existence of a pair of tentacular tufts

at the level of the middle of the trunk in *Pterosagitta*, a quite unique feature in the Aphragmophora, seems to remind us of various small sensory apparatus found on the body surface of *Spadella*.

The most problematical is the situation of the Flabellodontina. The body of *Krohnitta* is adapted to the planktonic life as well as that of *Flaccisagitta* of the Ctenodontina. It is flaccid enough and devoid of any collarette or glandular structures on the body surface. The corona ciliata is confined on the neck; this may be accepted as the sign of a primitive feature. Whereas the structure of hooks, especially that of teeth, is quite unique in the extant chaetognaths. It is not common to the Ctenodontina nor to any members of

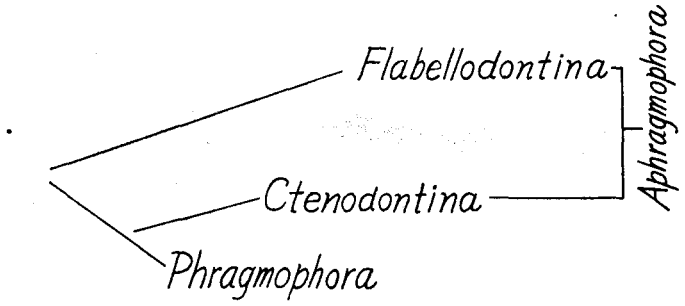


Fig. 2. Diagram showing a possible relation among chaetognath orders and suborders.

the Phragmophora. In the armature structure, the Ctenodontina is related closely to the Phragmophora. Thus, at present, the Flabellodontina is included in the Aphragmophora only for convenience's sake, on the basis of its having no ventral transverse musculature. This does not mean that Flabellodontina is derived from the Ctenodontina nor that these two groups had a common ancestor phylogenically very significant. Rather, it is very possible that the Flabellodontina belongs to another strain else than that comprising the recent Phragmophora and Ctenodontina, branched off from the further remote ancestral form and specialized along the way to adapt itself to the planktonic life.

IV. The splitting of the former genus "*Sagitta*" and the phylogeny among the newly established genera

ALVARIÑO (1963) distinguished nine groups in the former genus "*Sagitta*". They are: (1) *maxima*-group comprising *maxima, lyra, gazellae* and *scrippsae*, (2) *hexaptera*-group comprising *hexaptera* and *enflata*, (3) *planctonis*-group including *planctonis, zetesios* and *marri*, (4) *serratodentata*-group including *serratodentata, pacifica, pseudoserratodentata, tasmanica* and *bierii*, (5) *bipunctata*-group

comprising *bipunctata* and *helenae*, (6) *euneritica*-group comprising *crassa*, *euneritica*, *euxina*, *friderici*, *peruviana*, *popovicii*, *setosa* and *tenuis*, (7) *hispida*-group including *ferox*, *hispida* and *robusta*, (8) *elegans*-group comprising *elegans*, *minima* and probably *decipiens*, and (9) *neglecta*-group including *neglecta*, *regularis* and *oceania*. *S. bedoti*, *S. pulchra*, etc. were left without being included in any of the groups defined above. She made this grouping on the basis of the general body appearance including the fin system, the structure of the seminal vesicle, existence or absence of the intestinal diverticula, the outline of the pigmented area of the eye and vertical and horizontal distributions of the animals. Very fortunately the outline of my subdivision of the former genus "*Sagitta*" conforms to hers, but a few points. I subdivided the former genus "*Sagitta*" into nine genera, too. In my treatment, however, the feature of the corona ciliata and the existence or absence of the rayless-zones on the lateral fins are also regarded as significant taxonomically, while the horizontal or vertical distributions are not considered to be a leading factor to separate groups. Thus the most remarkable discrepancies between ALVARIÑO's grouping and mine are found in the treatment of *S. crassa* and *S. minima*. ALVARIÑO included the former in the *euneritica*-group, but it is treated in my classification under the genus *Aidanosagitta*. She treated the latter together with *S. elegans*, but it is included in the genus *Mesosagitta* in my grouping.

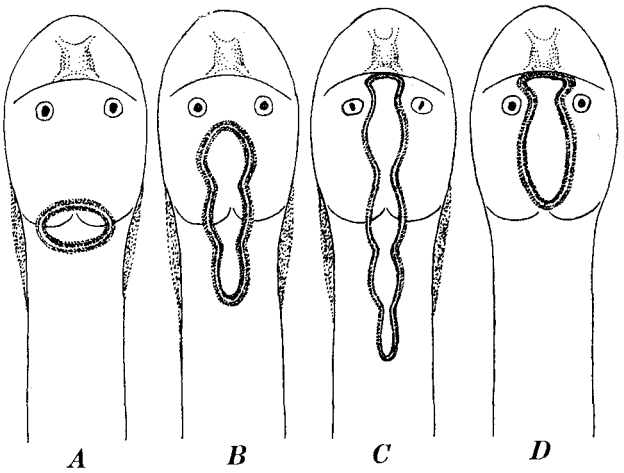
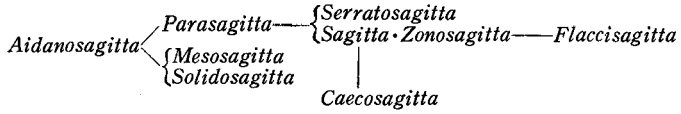


Fig. 3. Supposed serial modification of the corona ciliata. A—The most primitive state found in Spadellidae, Pterosagittidae and Krohnittidae. B—The most primitive state in Sagittidae, found in *Aidanosagitta*, *Mesosagitta* and *Solidosagitta*. C—The state common to *Sagitta* s. s., *Zonosagitta*, *Serratosagitta* and *Parasagitta*. D—The most specialized state found in *Flaccisagitta*.

Then, how are these nine new genera arranged phylogenically? As already mentioned in the paragraph II b), *Aidanosagitta* must be the most primitive group, whereas the most specialized form adapted to the oceanic plankton life may be *Flaccisagitta* which is characterized by flaccid body appearance, existence of remarkable rayless-zone on lateral fins, spherical to ellipsoidal seminal vesicle without any differentiated anterior glandular portion, complete degeneration of collarette and the corona ciliata confined to the head and stretched from the posterior edge of the brain to the neck. As to other genera, it is rather difficult to arrange them in a certain order phylogenically significant, because the generic characters of respective genera are intersected one another rather complicatedly. However, the absence or existence of the intestinal diverticula and the supposed serial modification of the corona ciliata* seem to make the following tentaive suppositions possible: (1) *Mesosagitta* and *Solidosagitta* are related to *Aidanosagitta*, (2) *Sagitta* s.s., *Zonosagitta* and *Serratosagitta* resemble one another very closely and related to *Flaccisagitta* probably via *Zonosagitta*, (3) *Parasagitta* may be situated between *Aidanosagitta* and the group comprising *Sagitta* s.s., *Serratosagitta* and *Zonosagitta*, and (4) *Caecosagitta* is possibly a form derived from the group of *Sagitta* and its allies and sunken to the depths. These relationships may be shown schematically in the following diagram.



* In Sagittidae, the serial modification seems to start from the state found in *Aidanosagitta* (Fig. 3B), being extended anteriorly beyond the level of the eyes to the posterior border of the brain (Fig. 3C) and at last attain the state found in *Flaccisagitta* (Fig. 3D) by shortening the length in the portion posterior to the neck.